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Molecular barley breeding

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Abstract Breeding progress in barley yield in the UK is being sustained at a rate in the order of 1% per annum against a background of declining seed sales. Commercial barley breeders are largely concentrating upon the elite local gene pool but with genotypic evidence suggesting that there is still considerable variation between current recommended cultivars, even those produced as half-sibs by the same breeder. Marker Assisted Selection (MAS) protocols could be substituted for conventional selection for a number of major-gene targets but, in the majority of cases, conventional selection is more resource efficient. Results from current QTL mapping studies have not yet identified sufficiently robust and validated targets for UK barley breeders to adopt MAS to assist in the selection of complex traits such as yield and malting quality. Results from multiple population mapping amongst the elite gene pool being utilised by breeders and from association studies of elite germplasm tested as part of the UK recommended list trial process do, however, show some promise.

Keywords Barley · Markers · Major genes · QTLs · Marker assisted selection

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Breeding progress

Barley breeding in the UK is very competitive with elite lines from some 20 European breeders being entered each year for National List trials. On average, over 35 spring and 40 winter barley lines have been entered each year since 1993. On average, 11 lines have been selected each year to progress from National to Recommended List Trials leading to an average of six new recommendations each year over both crops over the same period. The uptake of recommended cultivars has been highly variable and the average duration of placing on the recommended list over the period has been four years, although this figure does include cultivars that were coming to the ends and beginnings of their spans on the list at the start and end of the survey period respectively. Some cultivars, such as the winter barley Avenue have only been recommended for a single year but others, such as the winter barley Fanfare and the spring barley Optic have been recommended for more than 10 years. By using the UK seed certification figures from harvest 1983 to 2004, we can identify the most successful cultivars and their relative market impact. The accumulated production in tonnes over this period

shows that 16 spring and 14 winter barley cultivars exceeded 40,000 t and, as these accounted for over 75% of the total production over this period, can be judged as market successes (Table 1). Over this period, the annual production of certified barley seed has declined by over 60% from a peak of over 260,000t in 1987 to 106,000 in 2004. There are a number of potential reasons behind this decline such as an increase in Farm-Saved Seed and/or reforms to the Common Agricultural Policy. The decrease does, nevertheless, represent a real reduction in the potential return from plant royalties in barley breeding. A further change over the period has been the increasing dominance of a single cultivar in the production of certified seed with the current major cultivars, Optic (spring) and Pearl (winter) occupying over 50% of production, further reducing the market opportunities of breeders other than those of the leading cultivars.

A study of recommended list trials from 1993–2002 showed that breeding progress in yield of winter and spring barley was approximately 1% per annum for fungicide-treated trials (Thomas, 2003). We have extended this study to examine the effect of recommendations made in 2003 and 2004 and also considered data from untreated trials. Using the REstricted Maximum Likelihood (REML) directive in GENSTAT to estimate mean performance of each line in recommended list trials since 1993 and regressing that data against year of first recommendation shows that barley breeders are indeed continuing to make progress in breeding for both treated and untreated yield. Progress in both is in the order of 1% per annum and accounts for over 50 and 25% of the variation in the cultivar means of spring and winter barley respectively.

Commercial barley breeders are achieving this rate of progress by largely working within the elite gene pool. This generally leads to a high mid-parental value from each crop and thus a better chance of obtaining superior recombinant inbred lines. Whilst a broader cross may theoretically generate an even better recombinant, the chances of doing so and/or then selecting it are small so success is more likely to be derived from concentrating on crosses with a high mid-parent. Indeed, if one surveys the recommended list of spring and winter barley cultivars from the UK (www.hgca.com), one can find that the variation amongst the recommendations covers good expression of all the characters considered in the recommendation process. The recommended list cultivars Cocktail and Doyen are both derived, by the same breeder, from crosses with Linden and are thus half-sibs. Genotyping these two cultivars with 35 SSR markers revealed that at least 13 were polymorphic, leading to over 8000 different allelic combinations between these two closely related cultivars (Table 2). If one includes a third, but not directly related, cultivar (Troon), there are over 21 million different allelic combinations. Adding in two other cultivars that were both derived by the same German breeder and were also on the list of UK recommended spring barley cultivars

Table 1 Percentage of overall UK seed production from 1983–2004 of all barley cultivars for which > 40,000t seed was certified of spring and winter crop types

Cultivar	Type	Overall % seed production
Triumph	Spring	12.2
Optic	Spring	11.9
Chariot	Spring	8.9
Atem	Spring	8.5
GoldenPromise	Spring	4.6
Blenheim	Spring	4.2
Prisma	Spring	3.7
Camargue	Spring	3.3
Derkado	Spring	3.1
Alexis	Spring	3.1
Klaxon	Spring	2.6
Hart	Spring	2.6
Golf	Spring	2.6
Riviera	Spring	2.6
Tyne	Spring	2.4
Natasha	Spring	2.4
Igri	Winter	17.0
Pastoral	Winter	6.9
Marinka	Winter	6.6
Panda	Winter	5.9
Halcyon	Winter	5.7
Regina	Winter	5.4
Pearl	Winter	5.4
Fighter	Winter	4.7
Puffin	Winter	4.2
Magie	Winter	3.9
Intro	Winter	3.6
Pipkin	Winter	3.4
MarisOtter	Winter	2.6
Plaisant	Winter	2.3

Table 2 Number of polymorphic loci between each potential pairwise combination of five cultivars from the UK spring barley recommended list for 2005 from a survey with 35 SSR markers

	Doyen	Troon	Kirsty	Rebecca
Cocktail	13	15/16[a]	17/18	18
Doyen		18	19/20	20
Troon			19	16
Kirsty				14/15

[a]Two alleles were detected at a locus for some cultivars leading to the alternate possible polymorphic combinations

for 2005 (Table 2) increase the number of potential allelic combinations to over 1×10^{11} from just the five cultivars. Thus, whilst the amount of variation in the landrace and wild barley gene pools is undoubtedly far greater than that of the cultivated, there would appear to be more than sufficient variation to enable barley breeders to sustain breeding progress for the near future. Rasmusson and Phillips (1997) found that breeding advance was also being maintained in North American spring barley despite working with a narrow gene pool. Our genotyping results would suggest that this is indeed possible but is likely to be due to generation of new allelic combinations although a genotyping study of the material would be needed to confirm this.

Marker assisted selection

Major gene targets

The value of DH populations in barley genetic analysis has been highlighted by various authors since Choo and Reinbergs (1979) and was reviewed in a recent publication that identified some 23 barley populations that have been used to identify marker/trait associations for possible deployment in MAS (Forster & Thomas, 2003). The main advantage of doubled haploid populations in genetic analyses is the fact that they represent a fixed sample of the results of segregation from a cross and can therefore be widely distributed for estimating a wide range of phenotypes at many sites. In addition, the genotype can be directly related to the phenotype and therefore it is quite easy to carry out fresh DNA extractions for supplementary genotyping. The disadvantage is that routine production of large numbers (>200) of DH progeny from a single cross remains problematic and consumes considerable resources. Nevertheless, many more DH populations have been used in barley mapping since the last review (Forster & Thomas, 2003) with a significant effort from the Australian Barley Mapping Project (Langridge & Barr, 2003). There are now a large number of potential targets for deploying MAS either for major genes or QTLs.

There are, however, few examples of the use of MAS in commercial barley breeding. Perhaps the best example is the Barley Yellow Mosaic Virus complex where a variety of different markers have been developed (in DH populations) for selection of the rym4 and rym5 resistance genes (Table 3) and one, the SSR Bmac0029, is used by many European winter barley breeders. Markers are now available for several additional resistance loci and it is therefore possible to pyramid resistance genes in a MAS programme (Ordon et al., 2003). For many other major-gene disease resistances, phenotypic screening is often highly effective and there are few examples where MAS has been deployed as an alternative by commercial breeders. Even when working with major genes, it is important to validate marker/trait associations as even very closely linked markers may not prove to be reliable due to large discrepancies between the genetical and physical distances combined with selection for rare double recombinants. The fine-mapping (Pellio et al., 2005) and recent cloning of rym4/5 locus (Stein et al., 2005) opens up the prospect of a diagnostic marker for rym4/5-based virus-resistance.

Table 3 Development of molecular markers for potential use in selection for the rym4 and rym5 alleles for resistance to Barley Yellow Moasic Virus

Marker type	Reference
Restriction Fragment Length Polymorphism	(Graner & Bauer, 1993)
Sequence Tagged Site	(Bauer & Graner, 1995)
Random Amplified Polymorphic DNA	(Weyen et al., 1996)
Simple Sequence Repeat	(Graner et al., 1999)
Single Nucleotide Polymorphism	(Meyer et al., 2000)
Candidate Gene	(Wicker et al., 2005)

For quality targets, direct gene markers are available for some traits, such as beta-amylase thermostability (Kihara et al., 1998), but the value of this attribute in European germplasm appears to be limited. The frequency of the high thermostability Sd2H allele detected in a sample of over 500 EU spring barley cultivars peaked in the 1960's and 1970's but has since been in decline and was not detected in any of the 67 (including 41 spring) varieties from the study that were released since 1990 (E. Chiapparino, P. Donini, D O'Sullivan, unpublished results). A recent comparison of a random set of lines that segregated for the high thermostability Sd2H allele showed that it did not have a significant effect upon either Hot Water Extract or Fermentability (Dr J. Swanston, SCRI, pers. comm.). A marker for selection of non-producers of epiheterodendrin, a characteristic of importance to Scotch Whisky production, was reported by Swanston et al. (1999) and has been used by a number of barley breeders. The closest marker (Bmac213) was, however, some 5 cm from the gene and a number of cultivars, such as Decanter, were recombinants between the marker and the target gene thus limiting its application. Recently, a potential direct gene marker has been developed which appears to be diagnostic for the trait (Dr P. Hedley, SCRI, pers. comm.) and so it should now be possible for barley breeders to use MAS for reliable identification of non-producers of epiheterodendrin.

QTL targets

Important traits such as yield and malting quality are controlled by a number of genes that not only interact with each other but also with the environment. Breeders therefore need to conduct multi-site trials to ensure that they get an accurate estimate of a phenotype but this is, of course, expensive and can only be carried out in the latter stages of a breeding programme. The identification of key genomic regions controlling such traits and the development of MAS protocols as a surrogate selection scheme is therefore attractive and considerable effort has been expended upon QTL mapping in barley since the first whole genome survey published in 1992 (Heun, 1992). Forster and Thomas (2003) identified some 23 barley DH populations that had been used in QTL mapping and a considerable number of further populations have since been developed e.g. Langridge and Barr (2003).

Validation of QTLs has, however, received comparatively little attention. Some studies have focused upon re-detecting a QTL in a further sample of the cross used to detect it (e.g. yield in Steptoe × Morex (Romagosa et al., 1999)) but proper validation requires testing in another cross. The Australian Barley Mapping Programme has devoted considerable effort in developing MAS protocols for barley that have been successfully used to introgress gene/QTL targets from the wider gene-pool into an Australian background. In North West Europe, breeders are largely concentrating upon crosses made within the local elite gene pool and thus require a successful demonstration that markers can not only be associated with variation for complex traits but also be used in MAS protocols. Studies in DH populations from crosses such as Blenheim × E224/3 (Thomas et al., 1995; Thomas et al., 1996), Blenheim × Kym (Bezant et al., 1997a; Bezant et al., 1996; Bezant et al., 1997b) and Derkado × B83-12/21/5 (Thomas et al., 1998) and a RIL population from Tankard × Livet (Rajasekaran et al., 2003) have clearly demonstrated that QTLs can be detected in the elite North West European gene pool but there are few examples of QTLs that have been validated in another cross.

Considering the North American barley gene pool, a QTL allele on chromosome 5H from Morex increased alpha-amylase activity in the Steptoe × Morex mapping population (Hayes et al., 1993). Ayoub et al. (2003) created an independent population from a cross between Morex and the feed cultivar Labelle and applied MAS at two loci in the region of the QTL. The mean alpha-amylase activity of lines that had been selected for the Morex alleles at the two loci was significantly greater than that of lines with the Labelle alleles, indicating that the MAS approach had been successful. In contrast, a QTL for fermentability was identified on chromosome 5H in the Derkado × B83-12/21/5 DH population with the increasing allele derived from B83-12/21/5 parent with the poorer malting quality (Swanston et al., 1999). A doubled haploid backcross population was constructed from a donor line within the population and an elite potential malting quality cultivar as the recipient. The population was genotyped with molecular markers flanking the QTL but phenotypic analysis of the means and ranges of the genotypic groups so formed did not reveal any significant effects of the donor alleles (Meyer et al., 2004)). The latter study suggested that QTL that were effective in a poor quality background may not be effective in a

good background because their function may not be required. For instance, the QTL detected in the Derkado × B83-12/21/5 population may have been effective in a high protein background but of no value in the low protein background of a typical malting barley cultivar.

The same character has often been studied in different DH populations and, in such cases, some form of co-location of QTLs would suggest that these were potential QTL targets for MAS. A comparison of QTL locations for yield and hot water extract from 8 mapping populations did not provide very strong evidence of co-location for either character. The most frequently detected region was on chromosome 1H for hot water extract but the overall span of the confidence intervals for the QTLs detected in five populations was equivalent to a chromosome arm (Thomas, 2003). When one considers the potential location of favourable QTL alleles for other characters in repulsion in this region then it is far from an ideal target for MAS. Clancy et al. (2003) conducted a similar study for beta-amylase activity and diastatic power for three North American barley DH mapping populations, Steptoe × Morex, Harrington × TR306 and Harrington × Morex. Given the fact that the parents used ensured that all three populations were connected and that the traits chosen were less complex than yield or hot water extract, one would expect some co-location of QTLs. QTLs were detected in 14 gross genomic regions and there was some evidence of co-location in four of these but never for more than two crosses. These four regions would, however, represent potential targets for MAS.

One of the main problems in comparing results from different QTL studies is that most are carried out in different environments, whether years or sites. We therefore obtained seed of the Steptoe × Morex DH mapping population and grew that in a trial at the SCRI site alongside another trial of the Derkado × B83-12/21/5 DH mapping population. The trials were grown in a single replicate Modified Augmented Type 2 designs each year from 2002 to 2004 inclusive in plots 2.5 m long × 1.5 m wide (including gaps) sown with 40 g seed. The trials were managed according to local fungicide and fertiliser practice for spring malting barley and all plots were harvested with a small plot combine when ripe. The harvested seed was cleaned and graded over a 2.5 mm sieve and sub-samples were analysed for milling energy using the Comparamill (Allison et al., 1979). Analysis of the genotypic means for each year revealed highly significant genetic variation for milling energy in both populations but only the Derkado × B83-12/21/5 population was sensitive to the differences between the three growing seasons (Table 4). The overall means for each DH within each population were then used to search for QTLs using PLABQTL (Utz & Melchinger, 1996), as described by Rajasekaran et al. (2003). A revised map and genotypic data for the Derkado × B83-12/21/5 DH population (Chloupek et al., 2005) and the publicly available data for the Steptoe × Morex DH population (http://gnome.agrenv.mcgill.ca/basemaps.html#SMbasemap) were used in the QTL analyses. Eight QTLs were detected, six from the Steptoe × Morex population and two from Derkado × B83-12/21/5 but none were co-located (Figure 1). Milling Energy was chosen as the example because it is a highly heritable character and has not been subject to a long history of direct selection and so, despite the differences in gene-pools, might be expected to show some co-location of QTLs. Milling Energy was also measured on other DH mapping populations grown in trials at SCRI and the National Institute of Agricultural Botany (NIAB) from 2002 to 2004 as part of a study of multiple cross mapping amongst current elite UK barley genotypes (Rae et al., 2004). As several alleles were detected at the marker loci used to genotype the multiple crosses, we adopted a stepwise forward multiple regression approach to detect QTLs. Each allele at each marker locus was converted into a binary marker according to whether or not it possessed that allele so that the number of potential binary variates per marker locus was equal to the number of alleles detected (Casas et al., 2003). A number of alleles were detected at a low frequency (<5%) and these were eliminated from the analysis. This analysis detected a number of loci for Milling Energy, the most important of which was located in Bin 2 of chromosome 3H, i.e. potentially

Table 4 Mean milling energies (Joules $5\,g^{-1}$) for Derkado × B83-12/21/5 (D × B) and Steptoe × Morex (S×M) DH mapping populations grown in trials for three years at SCRI and significance of main effects

	Population Mean in Year			Significance Level	
Population	2002	2003	2004	Genetic	Years
D × B	720.0	662.1	611.5	<0.001	<0.001
S × M	765.6	761.2	758.3	<0.001	NS

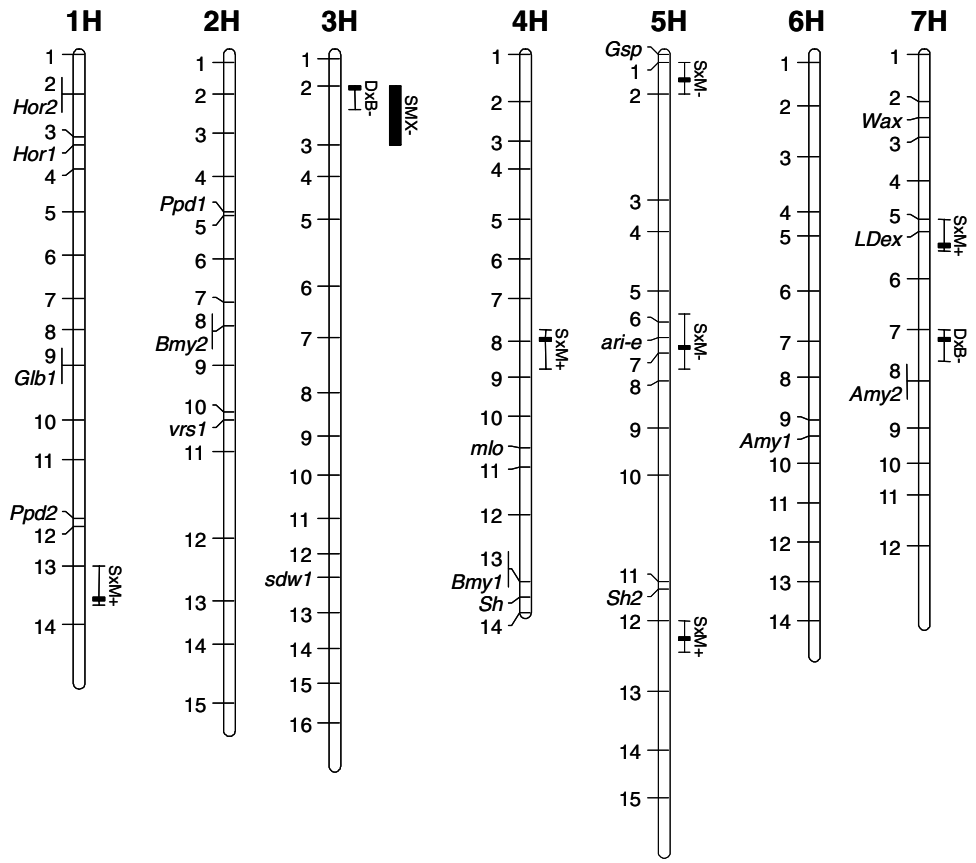

Fig. 1 Milling energy QTL placed on Steptoe × Morex (S×M) QTL Bin map for milling energy. Thick line indicates QTL peak and whiskers its 1 LOD confidence interval for Derkado × B83-12/21/5 (D×B) and S × M mapping populations. Thick bar indicates bin location of most significant QTL from a mutiple cross study (SMX). Sign indicates effect of alleles from the first named parent

co-located with one of the QTL from the Derkado × B83-12/21/5 population (Figure 1).

The key question for plant breeders is to identify markers for QTLs that are relevant to their germplasm. The multiple cross mapping approach described above is a potential route to identifying relevant markers for use in MAS. Association genetics studies amongst elite cultivars is another route and has been applied to spring barley lines entered into official Danish trials (Kraakman et al., 2004) to identify QTLs for yield and yield stability. This approach is also highly promising and can be used to identify genomic regions that have been preserved in selection for complex traits. For instance, as part of another larger study, Macaulay et al. (2004) had genotyped 41 UK winter barley lines that had been entered into Recommended List trials from 1993–2000. Hot water extract data from these trials was made available to us by permission of Crop Evaluation Limited and we combined it with the genotypic data in a single marker ANOVA to identify seven SSR loci that were significantly associated with the character. Maris Otter was a major step forward in winter barley malting quality and was first recommended in 1965 and is still grown for some specialist malting purposes. When its genotype is compared to that of Pearl, the current leading winter barley malting cultivar by tonnage bought (www.ukmalt.com), one finds it shares alleles at six of these seven loci (Table 5). Maris Otter features in the pedigree of Pearl through Puffin, suggesting that specific alleles at these loci are essential in the selection of hot water extract. Three of the Maris Otter alleles were the most frequently detected amongst the SSR loci for the UK winter barley recommended list entries but these apparently had minor effects. The two SSR alleles with the largest effect on hot water extract for Maris Otter were the second most frequently detected

Table 5 Allelic composition by frequency of Maris Otter, Puffin and Pearl at seven SSR loci significantlty associated with hot water extract and the estimated effect of the Maris Otter allele

	SSR1	SSR2	SSR3	SSR4	SSR5	SSR6	SSR7
Maris Otter	b	b	a	f	a	d	a
Puffin	b	a	a	b	–	d	g
Pearl	b	b	a	b	–	d	a
Maris Otter Allele Effect	1.1	1.5	0.7	0.2	0.7	1.4	−0.3

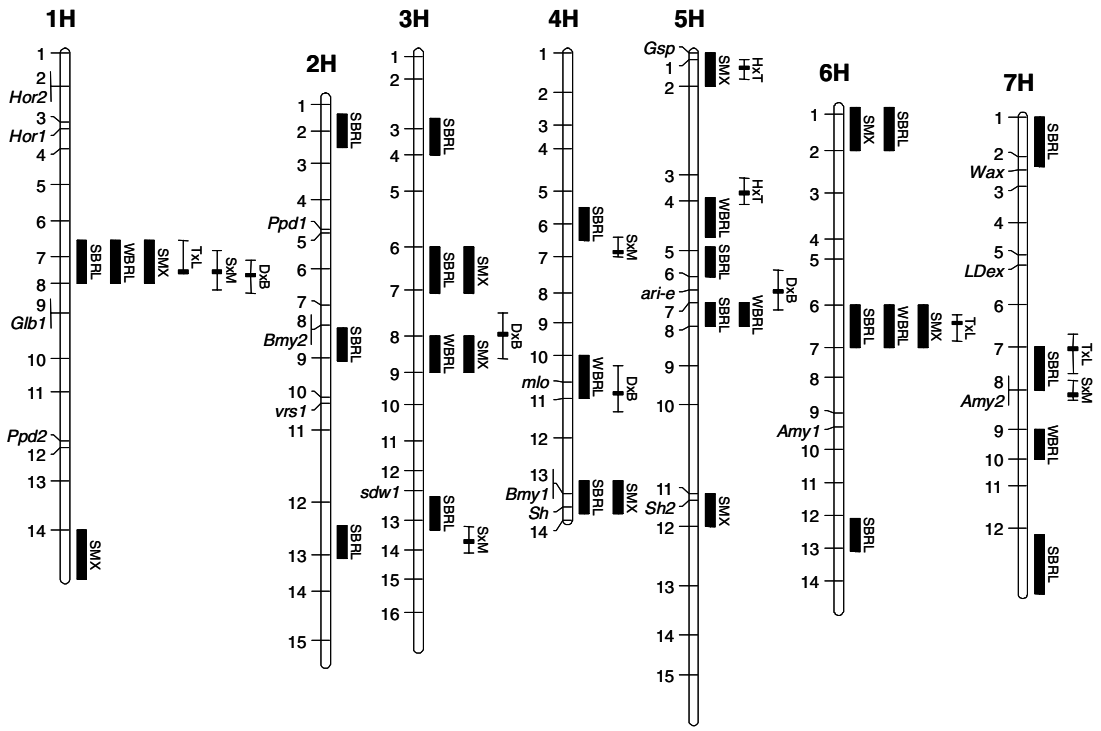

Fig. 2 QTL bin map for hot water extract based on data from ANOVA of spring (SBRL) and winter barley (WBRL) recommended list data, data from multiple regression analyses of multiple populations (SMX) and interval mapping of Steptoe × Morex (S×M), Harrington × TR306 (H×T), Derkado × B83-12/21/5 (D×B) and Tankard × Livet (T×L) mapping populations. Thick bar indicates bins spanned by a significant marker and, for interval mapping, QTL peaks indicated by thick line and 1 LOD confidence intervals by whiskers

with the most frequent alleles in this germplasm group either having a large negative or negligible effect.

Conclusions

A number of molecular markers have been associated with either major genes or QTLs controlling key traits in barley using mainly DH populations specifically targeted to one or more of these traits. The penetrance of MAS into mainstream barley breeding, especially for crosses within an elite gene pool specific to a geographic region, is poor and largely confined to major gene targets. Part of the problem is that the diversity of the crosses used to map a trait renders the results inapplicable to the elite gene pool. Alternative approaches, such as the use of multiple populations from crosses within the elite gene pool and association genetics analyses of elite germplasm, appear more likely to produce results of value for deployment in MAS. Certainly the results from the two studies described above show some co-location of hot water extract QTLs, notably in the centromeric regions of chromosomes 1H and 5H (Figure 2).

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References

Allison MJ, Cowe IA, Borzucki R, Bruce F, McHale R (1979) Milling energy of barley. J Inst Brewing 85:262–264

Ayoub M, Armstrong E, Bridger G, Fortin MG, Mather DE (2003) Marker-based selection in barley for a QTL region affecting alpha-amylase activity of malt. Crop Sci 43:556–561

Bauer E, Graner A (1995) Basic and applied aspects of the genetic analysis of the ym4 virus resistance locus in barley. Agronomie 15:469–473

Bezant JH, Laurie DA, Pratchett N, Chojecki J, Kearsey MJ (1997a) Mapping of QTL controlling NIR predicted hot water extract and grain nitrogen content in a spring barley cross using marker-regression. Plant Breed 116:141–145

Bezant J, Laurie D, Pratchett N, Chojecki J, Kearsey M (1996) Marker regression mapping of QTL controlling flowering time and plant height in a spring barley (Hordeum vulgare L.) cross. Heredity 77:64–73

Bezant J, Laurie D, Pratchett N, Chojecki J, Kearsey M (1997b) Mapping QTL controlling yield and yield components in a spring barley (Hordeum vulgare L.) cross using marker regression. Molecular breed 3:29–38

Casas AM, Moralejo MA, Yahiaoui S, Ciudad F, Codesal P, Montoya JL, Molina-Cano JL, Gracia MP, Lasa JM, Igartua E (2005) Marker-trait associations in barley. In Integrated quantitative and molecular genetics in plant breeding. Abstracts of 12th meeting of the Eucarpia section of biometrics in plant breeding. pp 91–92

Chloupek O, Forster BP, Thomas WTB (2005) The effect of semi-dwarf genes on root system size in field grown barley. Theor Appl Genet (in press)

Choo TM, Reinbergs E (1979) Doubled haploids for estimating genetic variances in presence of linkage and gene association. Theor Appl Genet 55:129–132

Clancy JA, Han F, Ullrich SE (2003) Comparative mapping of beta-amylase activity QTLs among three barley crosses. Crop Sci 43:1043–1052

Forster BP, Thomas WTB (2003) Doubled haploids in genetic mapping and genomics. In: Maluszynski M, Kasha KJ, Forster BP, Szarejko I Dordrecht (eds) Doubled haploid production in crop plants. Kluwer, The Netherlands, pp 367–390

Graner A, Bauer E (1993) Rflp mapping of the Ym4 virus-resistance gene in Barley. Theor Appl Genet 86:689–693

Graner A, Streng S, Kellermann A, Schiemann A, Bauer E, Waugh R, Pellio B, Ordon F (1999) Molecular mapping and genetic fine-structure of the *rym5* locus encoding resistance to different strains of the Barley Yellow Mosaic Virus Complex. Theor Appl Genet 98:285–290

Hayes PM, Liu BH, Knapp SJ, Chen F, Jones B, Blake T, Franckowiak JD, Rasmusson DC, Sorrells M, Ullrich SE, Wesenberg D (1993) Quantitative trait locus effects and environmental interaction in a sample of North American barley germ plasm. Theor Appl Genet 87:392–401

Heun M (1992) Mapping quantitative powdery mildew resistance of Barley using a restriction-fragment-length-polymorphism. Map Genome 35:1019–1025

Kihara M, Kaneko T, Ito K (1998) Genetic variation of beta-amylase thermostability among varieties of barley, Hordeum vulgare L., and relation to malting quality. Plant breed 117:425–428

Kraakman ATW, Niks RE, Van den Berg PMMM, Stam P, van Eeuwijk FA (2004) Linkage disequilibrium mapping of yield and yield stability in modern spring barley cultivars. Genet 168:435–446

Langridge P, Barr AR (2003) Better barley faster: the role of marker assisted selection - Preface. Aust J Agricultural Res 54:1–4

Macaulay M, Ramsay L, Russell J, Marshall D, Waugh R, Thomas W (2004) Molecular markers to analyse breeding progress in barley. Aspects of Appl Biol 72:139–146

Meyer RC, Lawrence PE, Young GR, Thomas WTB, Powell W (2000) SSRs and SNPs – diagnostic tools for Barley yellow mosaic virus. In: logue S (ed) Barley genetics VIII, proceedings of the 8th international Barley genetics symposium, vol II. Dept Plant Sciences, Adelaide University, Adelaide, Australia, pp 144–146

Meyer RC, Swanston JS, Brosnan J, Field M, Waugh R, Powell W, Thomas WTB (2004) Can anonymous QTLs be introgressed successfully into another genetic background? results from a Barley malting quality parameter. In: Spunar J, Janikova J Kromeriz (eds) Barley Genetics IX, vol II. Agricultural Research Institute, Czech Republic, pp 461–467

Ordon F, Werner K, Pellio B, Schiemann A, Friedt W, Graner A (2003) Molecular breeding for resistance to soilborne viruses (BaMMV, BaYMV, BaYMV-2) of barley (Hordeum vulgare L.). Zeitschrift fur Pflanzenkrankheiten und Pflanzenschutz-Journal of Plant Diseases and Protection 110:287–295

Rae SJ, Keith R, Leigh F, Mackie A, Matthews D, Felix G, Morris PC, Donini P, Thomas WTB (2004) Small mapping crosses and their use to establish a broad based QTL map for barley. In: Spunar J, Janikova J Kromeriz (eds) Barley Genetics IX, vol II. Agricultural Research Institute, Czech Republic, pp 195–200

Rajasekaran P, Thomas WTB, Wilson A, Lawrence P, Young G, Ellis RP (2003) Genetic control of grain damage in a spring barley mapping population. Plant breed 123:17–23

Rasmusson DC, Phillips RL (1997) Review and interpretation: Plant breeding progresss and genetic diversity from de novo variation and elevated epistasis. Crop Sci 37(2):303–309

Romagosa I, Han F, Ullrich SE, Hayes PM, Wesenberg DM (1999) Verification of yield QTL through realized molecular marker- assisted selection responses in a barley cross. Molecular breed 5:143–152

Pellio B, Streng S, Bauer E, Stein N, Perovic D, Schiemann A, Friedt W, Ordon F, Graner A (2005) High-resolution mapping of the Rym4/Rym5 locus conferring resistance to

the barley yellow mosaic virus complex (BaMMV, BaYMV, BaYMV-2) in barley (Hordeum vulgare ssp. vulgare L). Theor Appl Genet 110:283–293

Stein N, Perovic D, Kumlehn J, Pellio B, Stracke S, Streng S, Ordon F, Graner A (2005) The eukaryotic translation initiation factor 4E confers multiallelic recessive Bymovirus resistance in Hordeum vulgare (L.). Plant J 42:912–922

Swanston JS, Thomas WTB, Powell W, Young G, Lawrence P, Ramsay L, Waugh R (1999) Using molecular markers to determine barleys most suitable for malt whisky distilling. Molecular breed 5(2):103–109

Thomas WTB (2003) Prospects for molecular breeding of barley. Ann Appl Biol 142:1–12

Thomas WTB, Baird E, Fuller JD, Lawrence P, Young GR, Russell J, Ramsay L, Waugh R, Powell W (1998) Identification of a QTL decreasing yield in barley linked to Mlo powdery mildew resistance. Molecular breed 4:381–393

Thomas WTB, Powell W, Swanston JS, Ellis RP, Chalmers KJ, Barua UM, Jack P, Lea V, Forster BP, Waugh R, Smith DB (1996) Quantitative trait loci for germination and malting quality characters in a spring barley cross. Crop Sci 36:265–273

Thomas WTB, Powell W, Waugh R, Chalmers KJ, Barua UM, Jack P, Lea V, Forster BP, Swanston JS, Ellis RP, Hanson PR (1995) Detection of quantitative trait loci for agronomic, yield, grain and disease characters in spring barley (*Hordeum vulgare L.*). Theor Appl Genet 91:1037–1047

Utz HF, Melchinger AE (1996) PLABQTL: a program for composite interval mapping of QTL. J Agricultural Genomics 2

Weyen J, Bauer E, Graner A, Friedt W, Ordon F (1996) RAPD-mapping of the distal portion of chromosome 3 of barley, including the BaMMV/BaYMV resistance gene ym4. Plant breed 115:285–287

Wicker T, Zimmermann W, Perovic D, Paterson AH, Ganal M, Graner A, Stein N (2005) A detailed look at 7 million years of genome evolution in a 439 kb contiguous sequence at the barley Hv-eIF4E locus: recombination, rearrangements and repeats. Plant J 41:184–194